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Genetic Variability of the Wing-Form Response to Photoperiod in a Subtropical Population of the Ground Cricket, *Dianemobius fascipes*

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ABSTRACT—*Dianemobius fascipes* is wing dimorphic, and its frequency of macroptery is controlled by photoperiod, temperature and larval density. In a local population of this cricket originated from Ishigaki Island (24°N, Japan), the genetic variability of the photoperiodic wing-form determination was assessed by examining 24 full-sib families. The percentage macroptery was highly variable among them, and its maximum occurring at 13 hr light/day (28°C, crowded) ranged from 15 to 95%. Although the basic pattern of the photoperiodic response was unchanged, the critical photoperiod was variable and inversely correlated with the general level of percentage macroptery. The heritability of the percentage macroptery was 0.7 in long days (≥ 13 hr light/day) but decreased to 0.3 in a short day of 11.5 hr, and that of the critical photoperiod was 0.36. In several mass-selected lines, the negative correlation between the critical photoperiod and the general level of percentage macroptery was confirmed. Selection for long-winged adults shortened the critical photoperiod and, conversely, selection for a short critical photoperiod increased the incidence of long-winged adults. The differences in the level of macropterism between the selected strains persisted in the responses to rearing density and temperature, but the response patterns to such non-photoperiodic cues were not modified by the selection. Thus, this local population holds a large amount of genetic variation in the liability to be macropterous, and the critical photoperiod varies in association with the genetic change in this liability, probably without any genetic shift of the threshold for the photoperiodic time measurement.

INTRODUCTION

In many wing-dimorphic insects, the wing form is determined by environmental and/or genetic factors. Environmental factors such as rearing density, photoperiod, temperature and food affect the wing form, and most wing-dimorphic insects are sensitive to more than one of these factors [6]. The genetic background of wing-form determination has been analyzed by selection and crossing experiments or comparison of geographic strains [20]. In many cases, polygenic systems are involved and the genetic mechanism may be complicated and diversified. Sex chromosomal and autosomal genes in crickets [14, 26], and major and modifier genes in hemipterans [7, 27] affect the ratio of the different wing forms. The complicated genetic modes are not unpredictable, because the wing form may be controlled by various environmental cues and each of the component responses to such cues is not a simple physiological process. For example, the photoperiodic response alone would consist of many physiological processes controlled by different genes [23]. In *Acronycta rumicis* [1], *Drosophila triauraria* [9] and *Chymomyza costata* [19], crossing experiments between local strains show the involvement of multiple loci in the photoperiodic response controlling diapause. This complexity might be the major difficulty to analyze the interaction between the genetic and environmental effects in the wing-form determination. In a few species such as *Nilaparvata lugens* [8], *Laodelphax striatellus* [16] and *Cavelerius saccharivorus* [4], however, the genetic control of the wing-form responses to rearing density has been studied.

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(24°N, Japan) shows a high genetic variability in the macropter/micropter ratio [14], but we had no information about its variability in the wing-form responses to environmental factors. We studied interactions between the genotype and environmental factors, particularly photoperiod, in this local population by using full-sib families and mass-selected lines. Based on the results obtained, we propose to view photoperiodic clines widely occurring in insects as a means of latitudinal adaptation without assuming genetic variation in the photoperiodic time measurement.

MATERIALS AND METHODS

In *Dianemobius* (formerly *Pteronemobius*) *fascipes,* the wing form (macropterous or micropterous) is affected by environmental [13], geographic [15] and genetic [14] factors. This species is widely distributed in Southeast Asia, and subtropical strains generally show higher levels of macroptery than tropical strains under suitable conditions for wing development. Crowding, long day and high temperature enhance macroptery.

We assessed the genetic variation and heritability of the photoperiodic wing-form determination by isolating cricket families. More than 100 males and females, collected in the subtropical island of Ishigaki (24°N, Japan) in November 1991, were allowed to mate at random. When their progeny reached the last larval instar, 24 male-female pairs were randomly chosen to establish full-sib families. About 100 larvae (the first generation) from each pair were reared in a long day of 14 hr light/day and the wing form was determined on adult emergence. In the following generations, 24 families were maintained by inbreeding of more than 20 pairs within each family. The photoperiodic response of each family was determined over ranges of 11–14 hr and 11.5–13.5 hr photophases with 30 minutes increments in the 2nd and 3rd generations, respectively. About 100 larvae were reared in a jar at each photoperiod. Twenty-four families were reared at the same time in each generation. The parents producing the 3rd generation were chosen from individuals reared in various photoperiods of 11–14 hr. Therefore, the photoperiodic conditions for parents were different between the 2nd and 3rd generations. However, we confirmed that the parental photoperiod did not affect the wing form of their offspring (unpublished observations).

We also determined the photoperiodic wing-form responses of three mass-selected lines. A laboratory stock culture was established with individuals collected in Ishigaki Island in February 1984, and have been maintained through a particular scheme of wing-form selection [14]. In this culture, the responsiveness to photoperiod was maintained by selecting micropterous adults in a short day of 12 hr and macropterous adults in a long day of 13 hr in alternate generations. After about 10 generations, the three lines designated as control (C), long-winged (L) and short-winged (S) lines were isolated. In the C line, the same selection scheme as that for the stock culture [14] was maintained. The original pattern and level of the photoperiodic response were well conserved in this line. In the L line, macropterous adults were selected under the short day, and in the S line, micropterous adults under the long day. The selection schemes for the C, L and S lines are shown in Fig. 1A in relation to the photoperiodic response curve of the original population. To confirm the involvement of a sex-linked gene(s) [14], we determined the photoperiodic responses of reciprocal hybrids between the L and S lines and 4 kinds of backcrosses.

We also attempted to select 3 lines with different critical photoperiods, shorter (θs) or longer (θl) than that in the original population, from the C and L lines. They were designated as θs (C), θl (C) and θs (L) lines. The θs (C) and θl (C) lines were isolated from the 19th generation of the C line, and the θs (L) line was separated from the 20th generation of the L line. In the θs (C) and θs (L) lines, selection for microptery at LD11 : 13 hr (11 hr light: 13 hr dark) and that for macroptery at LD12 : 12 hr were alternated in successive generations to obtain a shorter critical photoperiod between 11 and 12 hr. The θl (C) line was selected for microptery at LD13 : 11 hr and for macroptery at LD14 : 10 hr in alternate generations to obtain a longer critical photoperiod between 13 and 14 hr. In each generation of each line, more than 100 larvae were reared, and more than 10 pairs of

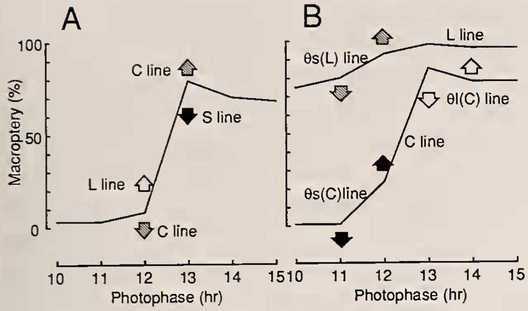

FIG. 1. Scheme of selection for control (C), long-winged (L), short-winged (S), short critical-photoperiod (θs) and long critical-photoperiod (θl) lines. The C, L and S lines were isolated from a laboratory culture derived from individuals collected in Ishigaki Island (24°N, Japan). The θs (L) line was separated from the L line, and the θs (C) and θl (C) lines from the C line. The arrows show the direction of selection at the photoperiods indicated by the horizontal axis. Upward arrows show selection for macroptery and downward ones selection for microptery. In the C, θs and θl lines, the direction of selection and photoperiod were alternated from one generation to the next as indicated. The curve in A represents the response of the unselected original population [13]. The curves in B represent the responses of the L and C lines determined in this study (see Fig. 7). For further explanation see text.

randomly chosen adults produced the next generation. Selection schemes are summarized in Fig. 1B. Photoperiodic response curves were determined in the 8th and 14th generations of the θs (C) line and the 6th and 12th generations of the θs (L) line but not in the θl (C) because the selection was ineffective.

In the standard rearing conditions, from 110 to 120 hatchlings were introduced into a 2-litre glass jar. The bottom of each jar was covered with dry sand, and 4 corrugated sheets of filter paper (diameter 11 cm) were piled up to increase the available surface. Dry insect feed (Oriental Yeast Industry, Tokyo) was provided ad libitum and sliced carrot at several-day intervals. Water was supplied in a vial with a cotton-wool plug. The jars were placed in wooden cabinets at 28 ± 1°C, and photoperiods were provided by 6 W fluorescent tubes regulated by timers. For rearings at lower densities, small plastic boxes ($10.5\times7.5\times6$ cm height) each containing a corrugated sheet of filter paper of 9 cm diameter were used. Other conditions were similar to those for the rearing with the glass jar.

RESULTS

Variation in photoperiodic response among 24 full-sib families

The photoperiodic response curves of the 24 full-sib families in the 2nd and 3rd generations are shown in Fig. 2. Under short days (<12 hr), the percentage macroptery was lower than 10% in all families but highly variable among families in long days (≥13 hr), ranging from 15 to 95% in both generations. The response patterns to photoperiod were similar among the families. The maximum incidence of macroptery occurred at LD13 : 11 hr, and the percentages of macroptery in different photoperiods were genetically correlated (Fig. 3). The critical photoperiod, defined here as the photoperiod at which the percentage macroptery is the midpoint between the upper and lower saturation levels, varied between 12 and 13 hr. The critical photoperiod and the percentage macroptery in long days (=the upper saturation level) seems to be genetically correlated (Fig. 4), although the correlation was significant only in the 2nd generation. When the two generations were pooled, the correlation was significant, and the higher the saturation level of macroptery, the

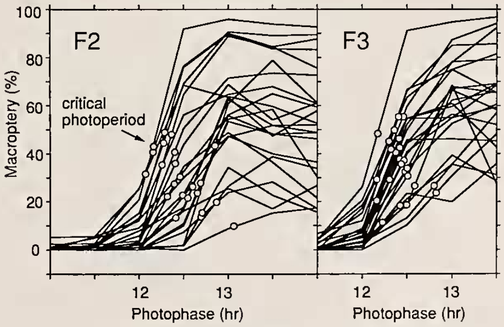

FIG. 2. Photoperiodic responses of 24 full-sib families of *D. fascipes* in the 2nd and 3rd laboratory generations under 28 ± 1°C and crowded conditions. The percentage macroptery in each family at each photoperiod was based on 70–110 adults. Circles indicate the critical photoperiod defined as the midpoint photoperiod between the upper and lower saturation levels of the percentage macroptery.

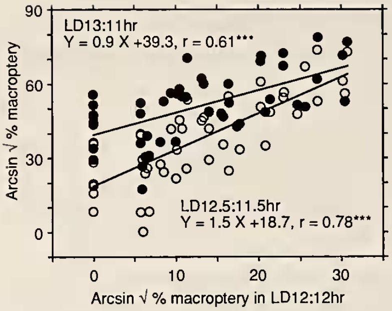

Fig. 3. Correlation between the percentages of macroptery in two different photoperiods among 24 full-sib families. Y is the percentage macroptery in the photoperiod indicated above the regression equation. Data for the 2nd and 3rd generations are pooled. *** Significant at $P \leq 0.001$.

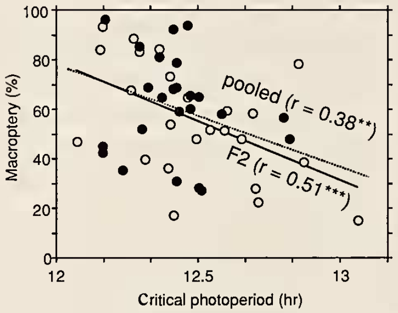

Fig. 4. Genetic correlation between the percentage macroptery in 13.5 hr photophase and the critical photoperiod in the 2nd (open circles) and 3rd (closed circles) generations of 24 full-sib families. The regression is significant in F2 ($P<0.01$) and pooled ($P<0.05$) generations but not in F3 ($P>0.05$).

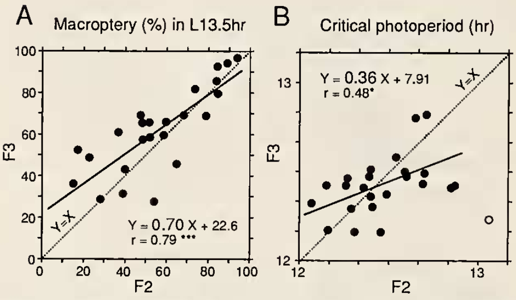

Fig. 5. Heritability estimates ($h^2=b$) of the percentage macroptery in a 13.5 hr photophase (A) and the critical photoperiod (B) derived from the 2nd and 3rd generations in 24 full-sib families. The hollow circle in B is excluded in computing the regression. *** Significant at $P \leq 0.001$, * $P \leq 0.05$.

shorter was the critical photoperiod.

The heritability of macroptery is determined from the regression of the 3rd generation on the 2nd generation by computing the coefficient [3]. Fig. 5A shows the offspring-parent regression for the percentage macroptery in LD13.5 : 10.5 hr. As in other wing dimorphic insects [20], this ground cricket showed a large phenotypic variation in the percentage macroptery, but the heritability was high (0.7) in long days ($\geq$13 hr) and decreased with shortening photoperiod (Fig. 6).

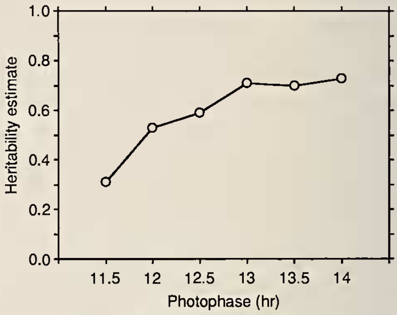

Fig. 6. Heritability estimates of percentage macroptery in different photoperiods in 24 full-sib families. Heritabilities in 11.5–13.5 hr photophases are derived from the 2nd and 3rd generation data and in 14 hr photophase from the 1st and 2nd generation data.

Fig. 5B shows the correlation in the critical photoperiod between the two generations. The heritability estimate was 0.20, but if only one family largely deviating from the general trend was excluded, the correlation between the two generations was significant and the heritability estimate was 0.36. The large deviation from the regression might be due to the limited number of tested photoperiods for determining the response curve. Fluctuations in the percentage macroptery near the critical photoperiod considerably affected the estimation of the critical photoperiod (see Fig. 2).

The total variance in the frequency of macroptery in the isolated families is analyzed in Table 1 using the data at 11.5 to 13.5 hr photoperiods available for both generations. The interactions between family and photoperiod, generation and photoperiod, and family and generation were all statistically significant. However, these interaction components of the variance were very small com-

TABLE 1. Variance analysis of the percentage macroptery (arcsine transformed) in the 2nd and 3rd generations of the 24 full-sib families reared under 11.5–13.5 hr photophases (see Fig. 2) For further explanation see text.

Source	SS	df	MS	F	P
Family	23394	23	1017	33.30	***
Photoperiod	90785	4	22696	743.14	***
Generation	444	1	444	14.54	***
Fam. × Phot.	7465	92	81	2.66	***
Fam. × Gen.	1774	23	77	2.53	***
Phot. × Gen.	399	4	100	3.27	*
Residual (F × P × G)	2810	92	31		

* $P<0.05$; *** $P<0.001$

pared with the photoperiod and family components. The large portion of the variance is due to photoperiod and family components, and the latter represents the genetic variation in the liability to be long (or short) winged. We can not explain the significant difference between the two generations. It might be due to slight uncontrollable differences in rearing conditions or genetic drift.

Photoperiodic responses in the mass-selected lines

Fig. 7 shows the responses of the L, S and C lines to 13 different photoperiods including DD (continuous darkness) and LL (continuous light). The frequency of macropterous forms was consistently different among the three lines over the whole range of photoperiods, i.e., the percentages of macroptery in different photoperiods are genetically correlated. Despite the large difference in the general level of macroptery among the three lines, their response patterns were similar. The percentage macroptery was the highest at LD13 : 11 hr and lowered sharply with decreasing photophase and reached the minimum level at LD11 : 13 hr. This low level was maintained to LD7 : 17 hr but gradually increased again toward DD. In the range of photophases longer than 13 hr, the percentage macroptery was slightly diminished but the high saturation level was more or less maintained from LD14 : 10 hr to LL. Thus the selection remarkably modified the level of macroptery but the basic pattern of the photoperiodic response curve was little changed.

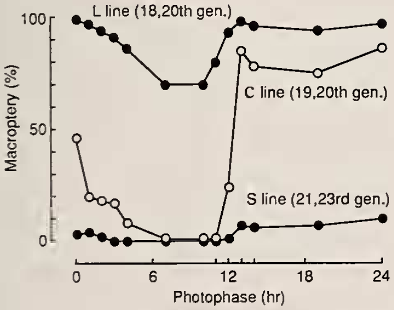

FIG. 7. Photoperiodic response curves of the C, L and S lines under 28 ± 1°C and crowded conditions. The data for the photophases shorter than 11 hr and for those longer than 10 hr were obtained in different generations as indicated for each line.

Photoperiodic responses in hybrids

The photoperiodic responses of reciprocal hybrids between the L and S lines and their backcrosses were intermediate between the parental lines (Fig. 8). The characteristics of the response with a maximum macroptery at LD13 : 11 hr and the critical photoperiod between 11 and 13 hr were retained in all hybrids and backcrosses. The reciprocal crosses (LxS vs. SxL) and reciprocal backcrosses (LxSL vs. SLxL or SxLS vs. LSxS) gave males differing in the incidence of macroptery, but the females were little affected by the reversed combinations of the parent lines. In this cricket the male is heterogametic (XO) and the female is homogametic (XX) [17]. The sexual difference as stated above, therefore, indicates that a certain locus (or loci) on the sex chromosome is at least partly involved in determining the incidence of macroptery.

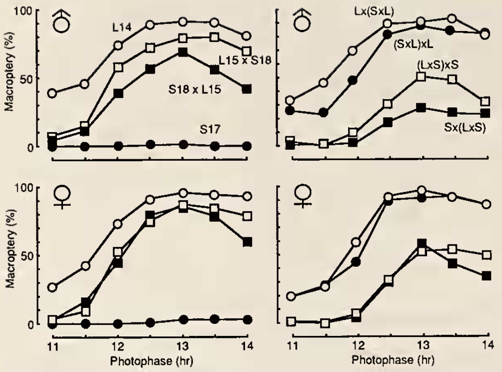

FIG. 8. The photoperiodic responses of reciprocal hybrids (left) between the long-winged (L) and short-winged (S) lines and the reciprocal backcrosses (right). Females are indicated first and the generation number for each selection line is given. More than 330 adults are involved in each datum point. The results with the male and female progenies are separately given to show the sex-linked effect.

The amplitudes of the photoperiodic response curves were larger in the hybrids than in either parent. In their percentages of macroptery, the hybrids were closer to the L line at LD13 : 11 hr and to the S line at LD11 : 13 hr.

Selection for critical photoperiod

The time courses of selection for the critical photoperiod are shown in Fig. 9. Although the percentage macroptery fluctuated from generation to generation, the difference in percentage macroptery between the two photoperiods, one longer and the other shorter than the selection goal of critical photoperiod, did not increase at all in the θs (L) and θl (C) lines. In the latter, the incidence of long-winged adults clearly decreased in both 13 hr and 14 hr photophases probably in response to the selection for short-winged adults in LD13 : 11 hr. The selection for long-winged adults in LD14 : 10 hr could not counteract this effect and failed to shift the critical photoperiod. The parallel decreases in percentage macroptery at LD12 : 12 hr and LD11 : 13 hr in the θs (L) line might be similarly due to selection for microptery at LD11 : 13 hr. On the other hand, a shorter shift of the critical photoperiod seemed to have occurred in the θs (C) line, for the difference in percentage macroptery between LD11 : 13 hr and LD12 : 12 hr increased across 12 successive generations (Fig. 9, middle).

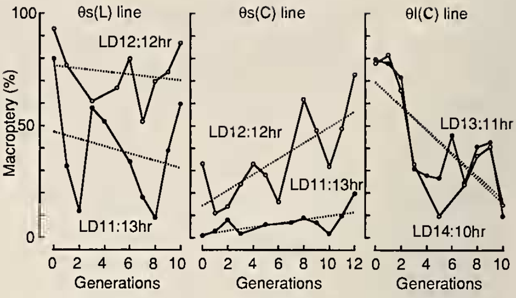

FIG. 9. Time courses of selection for critical-photoperiod in the θs(L), θs (C) and θl (C) lines. In each generation, the percentage macroptery was determined in two photophases just below (closed circles) and above (open circles) the selection-goal critical photophase. The dotted lines show regression across generations. The regression is significant ($P \leq 0.05$) in the θs (C) and θl (C) lines, but not in the θs (L) line. In the θs (C) line, the regression lines for LD12 : 12 and 11 : 13 hr were not parallel ($F = 6.08$, $P < 0.05$ in the test for parallelism). More than 100 adults are included in each datum point.

Fig. 10 compares the photoperiodic response curves of the θs (C), θs (L), C and L lines in the indicated generations. If the critical photoperiod is defined as the photoperiod at which the percentage macroptery is the midpoint between the upper and lower saturation levels, the critical photoperiods of the θs (C), θs (L) and L lines are about 1 hr shorter than that of the C line. The genetic correlation between the incidence of macroptery

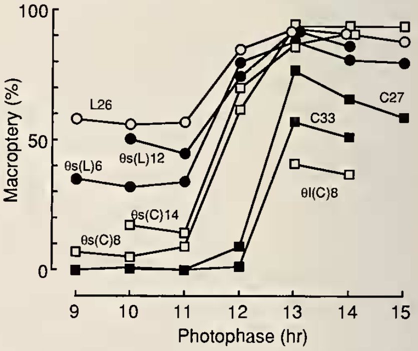

FIG. 10. Photoperiodic responses in the θs (L), θs (C) and θl (C) lines (see also Fig. 1 [B]). The numbers following the line codes indicate the generations. More than 300 adults are included in each datum point.

and the critical photoperiod (Figs. 2 and 4) was again clearly shown in these results. The shortening of the critical photoperiod was associated with an increase in the incidence of macroptery in the θs (C) line, and the increased incidence of macroptery with a decrease in the critical photoperiod in the L line.

Responses to rearing density and temperature

We tested the wing-form responses to rearing density in the L, S and C lines after more than 20 generations of selection (Fig. 11). Except for the S line, the effect of crowding on enhancing macroptery was obvious. Although the saturation levels were different, the response patterns to density in the C and L lines were similar. The C line at LD13:11 hr and the L line at LD10:14 hr showed similar saturation levels and similar threshold densities for inducing macroptery.

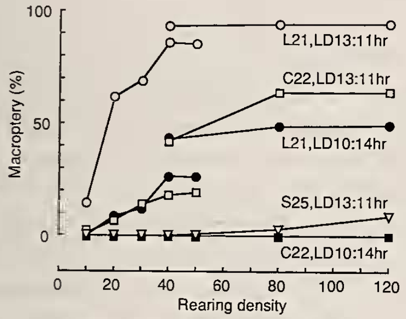

FIG. 11. Responses to rearing density in the C, L and S lines under LD10:14 and 13:11 hr at 28±1°C. Each line code is followed by the tested generation and photoperiod. More than 90 adults emerged at each density. The larvae were reared in plastic cases (10.5×7.5×6 cm height) at low densities (≤50 crickets/case) or cylindrical glass jars (2-litre capacity) at higher densities (≥40/jar).

The responses to temperature of the three selection lines are given in Fig. 12. The percentage macroptery was the highest at 27–28°C in all lines and thus their response patterns were similar. This indicates that the major difference in the percentage macroptery observed in the photoperiodic and density responses at 28°C among the selection lines were not due to any variation in the temperature threshold for inducing macroptery.

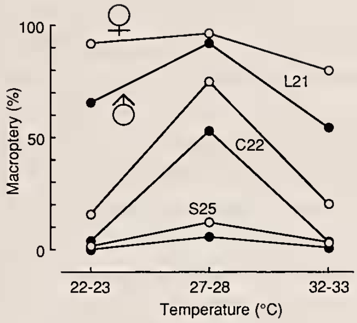

FIG. 12. Responses to temperature of the C, L and S lines under LD13:11 hr and crowded conditions. The numbers following the line codes show the generations. More than 320 adults emerged at each temperature in each line.

The results of these two series of experiments show that our scheme of wing-form selection did not shift either the thermal or the density threshold for macropterism. The established change in the incidence of macroptery should therefore be ascribed to a change in the liability to be macropterous.

DISCUSSION

Selection for a particular wing form under certain environmental conditions may give entirely different evolutionary consequences depending on the nature of genetic variability in the starting population. Iwanaga et al. [8] established lines of the planthopper *Nilaparvata lugens* with high and low incidences of the brachypterous form after 12–16 generations of selection. These lines were different mainly in the general level of brachyptery, but not in the response pattern and the response threshold of density. On the other hand, Fujisaki [4] reported that, in the bug *Cavelerius saccharivorus,* offspring of different wing forms showed different patterns of the response to rearing density with peaks of brachypter occurrence at different rearing densities. In this case, the original population had a genetic variation in the norm of response to density. *Dianemobius fascipes* is similar to *Nilaparvata lugens* in the response to wing-form selection. The differences in the macropter frequency among the selected lines or isolated families are not primarily due to the genetic variation in the threshold photoperiod, density or temperature (Figs. 7, 11, 12), but to the genetic variation in the liability to macroptery (or microptery).

In the Ishigaki population of *Dianemobius fascipes,* macropter frequencies under different photoperiodic conditions were genetically correlated. The large genetic variation in the response level may be partly due to this genetic correlation. Via and Lande [25] inferred that if expressions of a trait under different conditions are genetically highly correlated, the genetic variation in this trait is maintained or increased. Several factors such as mutation, super dominance, frequency-dependent selection, diversifying selection, heterogeneity and fluctuation in habitat conditions, etc. might also be responsible for maintaining or increasing the genetic variation in the wing-form liability [20, 21].

The photoperiodic response of an insect species tends to vary among local populations, and the critical photoperiod is usually correlated with latitude [1, 2, 10]. At least in some species such as *Acronycta rumicis* [1], *Drosophila triauraria* [9] or *Chymomyza costata* [19], crossing experiments between local strains show the involvement of multiple loci in the genetic control of photoperiodic response. Photoperiodic response may vary even within a local population and artificial selection effectively modifies the incidence of diapause [5, 22] or wing form [20] controlled by photoperiodic responses. However, artificial selection leading to variation in the most important parameter in the photoperiodic response, the critical photoperiod, has been reported only in a low-diapause laboratory stock of *Papilio zelicaon* [24].

We found the intra-population genetic variation of critical photoperiod in the Ishigaki population of *Dianemobius fascipes.* However, the critical photoperiod correlated with the response level. This can be clearly seen by plotting all the photoperiodic response curves obtained in this study (Fig. 13). They form a graded series with similar basic patterns, and the critical photoperiod shows a continuous variation within a narrow but ecologically important range of 11–13 hr. The higher the general level of macroptery, the shorter the critical photoperiod. This correlation already described for isolated families (Figs. 2 and 4) can be extended further by the results of mass selection. Thus, the critical photoperiod defined as the midpoint photoperiod between the upper and lower saturation levels of macroptery changed with the overall frequency of macroptery.

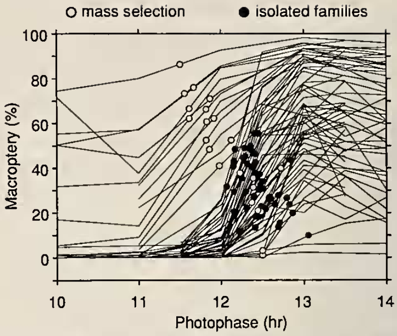

FIG. 13. All photoperiodic response curves obtained in this study are plotted to show the correlation ($r=0.74$, $P<0.001$) between the response level and critical photoperiod. The data for 24 full-sib families are replotted (closed circles). Open circles represent mass selected lines including the C, L, S, θs (L), θs (C), θl (C) lines and hybrids between the L and S lines. The critical photoperiod (open and closed circles) is defined as the photoperiod at which the percentage macroptery is the midpoint between the upper and lower saturation levels.

The stability of the photoperiodic response pattern and the variability of the critical photoperiod may give an interesting view of photoperiodic adaptation in insects. The critical photoperiod can be changed without variation in the photoperiodic time-measuring system. We hypothesize that the stability in the pattern of photoperiodic response is due to the genetic stability of the photoperiodic time-measuring system and that the observed shift of critical photoperiod is a result of change in the response level.

This hypothesis may be depicted by a threshold response model (Fig. 14). In this diagram, the photoperiodic time-measurement is kept unchanged, but the photoperiodically induced change in the liability is expressed by shifting the threshold lines along the liability axis. The variations in the photoperiodic response curve and critical photoperiod are thus envisaged from the genetic change in the liability distribution (Fig. 14, right). However, the physiological reality of the

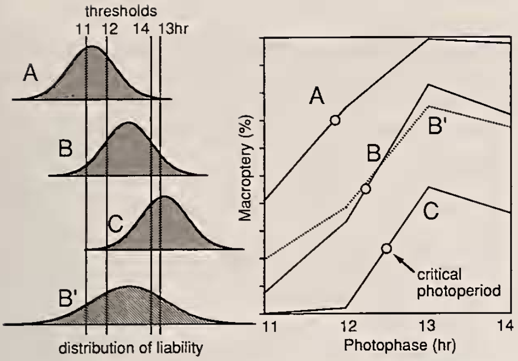

FIG. 14. Threshold response model [3] as adapted to interpret the variation in the photoperiodic wing-form determination of *D. fascipes*. The normally distributed liability for macroptery is genetically and environmentally determined. This may not necessarily be a single variable such as juvenile hormone titer; it can be a complex of different variables. The threshold divides the population into the two wing forms. If the liability of an individual is higher than the threshold, it becomes micropterous, and if lower, macropterous. In this model the photoperiodic time-measurement is assumed to be fixed and the photoperiodically induced change in the liability is expressed by shifting the threshold lines for different photoperiods. Populations A, B and C are different in the mean liability but the variance is fixed. B and B' are different in variance with the same mean. These liability distributions in relation to the threshold give photoperiodic responses as shown in the right panel. In alphabetical order, the overall level of percentage macroptery becomes lower, and the critical photoperiod becomes longer.

liability and threshold for the wing-form determination is yet to be elucidated.

Pittendrigh and Takamura [18] made a similar assumption in discussing the geographic adaptation in photoperiodism and circadian rhythm of *Drosophila auraria*. There is a clear correspondence between *Dianemobius* and *Drosophila*: the critical photoperiod varies with the photoperiodic response level. A similar trend of variation in the critical photoperiod was pointed out also by Saunders [23] in discussing the temperature effects on photoperiodic responses. Thus, these findings provide a new angle to view photoperiodic response curves in insects. The slope of the curve around the critical photoperiod may present the cumulative distribution of individual liabilities rather than individual threshold photoperiods (cf. [13, 22]).

The genetic correlation between the level of macropterism and the critical photoperiod within the ecologically significant range may influence the response to natural selection acting on either of these two parameters of adaptive significance. Selection for macroptery would change the critical photoperiod, and vice versa so that the selective response would be constrained by each other under certain circumstances. In northern Japan (>28°N), *Dianemobius nigrofasciatus*, a close relative of *Dianemobius fascipes*, occurs. The mode of its geographic variation in the photoperiodic wing-form determination seems to be similar to the intra-population variation of the Ishigaki strain of *D. fascipes*, although the critical photoperiod is longer than that in *D. fascipes*. *D. nigrofasciatus* maintains similar patterns of the wing-form response to photoperiod within its distribution range (28–44°N in Japan) despite a large variation in the general level of macroptery [11].

However, *D. nigrofasciatus* shows a clear geographic variation in the pattern of larval development response to photoperiod, the retarding effect being exerted by long days in the north but by intermediate days in the south [11]. A similar geographic variation in response pattern is also reported for the photoperiodic wing-form determination in *Dianemobius mikado* [12]. In these cases, the variation in response pattern is not associated with variation in responsiveness. Therefore, shifting distribution of liability is not the only way in which the photoperiodic response of insects can be modified under changing selection pressures. It is important to distinguish between the two different categories of genetic variation in understanding the evolution of photoperiodism in insects.

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